On the World-wide Dispersal of a Hawaiian Barnacle, *Balanus amphitrite hawaiiensis* Broch[1]

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IN RECENT YEARS a great deal of attention has been given by many workers, especially by marine ecologists and oyster planters, to the introduction of an Australian barnacle, *Elminius modestus* Darwin, into British waters and to its subsequent rapid spread along the continental European coasts from Brittany to the mouth of the Elbe River. The most recent extensive reviews of the occurrence of this barnacle on those coasts have been given by Den Hartog (1953) and Kühl (1954). Similarly, another instance of the introduction of an adventive barnacle into British coastal waters has also focused more attention on the possibility of other importations of many harmful foreign animals, as well as the extension of their natural geographical distribution. These studies strongly suggest that transportation on ships' bottoms or as stowaways among oysters is the chief means of migration (Allen, 1953; Coe, 1956).

The second example of a barnacle imported into European waters has long been considered to be *Balanus amphitrite* var. *denticulata* Broch, which was originally described by Broch (1927) from the Suez Canal. Since the first record of its occurrence on the southern coasts of Britain by Bishop (1950), most of the European workers, especially field ecologists who are not acquainted with the Pacific species of barnacles, have overlooked the fact that it is identical with *Balanus amphitrite* forma *hawaiiensis* Broch (1922), which is thought to be native to the Hawaiian Islands.

The object of this paper is to state the reasons for considering both of these forms as identical, at least with each other and possibly with other forms (or subspecies); and to present the alleged distribution of these related forms, as far as can be determined from the records of their occurrence.

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IDENTITY OF SUBSPECIES *denticulata* WITH SUBSPECIES *hawaiiensis*

Balanus amphitrite Darwin (1854) comprises many local forms, occasionally treated as either "subspecies" or "varieties," which are diversified in the number of teeth on the labrum. Most of the subspecies have only three teeth on each side of a median notch. The other subspecies almost always have four teeth, or a larger number (Hiro, 1938). Even in the subspecies having three or four teeth, the actual number is apt to vary among specimens, but in such cases the innermost one is either small or only rudimentary.

The two subspecies, *hawaiiensis* and *denticulata,* have such a multidenticulate labrum. The same is true of *Balanus eburneus* Gould and of *B. improvisus* Darwin, which are found as migrants on ships sailing between America and Europe. The number of teeth is also variable, ranging between 8 and 20; in most cases 10 to 13 larger teeth are found on each side, but never fewer than 8.

The most outstanding features in external ap-

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pearance which prove the identity of both forms are the colored stripes on the wall and the shape of the opercular valves. The shell is glossy white, smooth, and furnished with dark violet longitudinal stripes not crossed by any transverse stripes, though growth lines are faintly defined. Usually a broad white area is present in the middle of the larger compartments (carina, laterals, and rostrum), and a similar white area is present along both sides, the colored stripes being indistinct or quite absent there (see Table 1). The parietal tubes (the number of which corresponds with the number of the colored stripes, both distinct and obsolete) are narrow and numerous; the longitudinal septa on the inner lamina are strongly developed and run up to the sheath as high ridges which are very finely denticulate on both sides. The radii are very broad, with summits almost parallel to the base (Fig. 1).

In describing the new variety *denticulata* from the Suez Canal, Broch (1927) did not mention its close affinity with his earlier form *hawaiiensis* described in 1922. A comparison of his descriptions and figures of both forms with the Japanese specimens of *hawaiiensis* clearly shows that there is no difference important enough to separate them as different subspecies. Therefore, I believe that *denticulata* must be the same as *hawaiiensis*.

DIFFERENCES BETWEEN SUBSPECIES *hawaiiensis* AND SUBSPECIES *communis*

Notwithstanding the peculiarities mentioned above, sometimes there has been confusion among cirripede systematists between forma *hawaiiensis* (or *denticulata*) and Darwin's variety *communis* (see Table 3).

For example, Nilsson-Cantell (1938: 37) recognized both subspecies as distinct, but mentioned that "I do not consider it impossible that they (*denticulata*) represent a special race from the canal zone, but I do not think that numerous teeth on the labrum are a special characteristic of the subspecies *denticulata*." He emphasized that a great variability in the number of teeth on the labrum is not always of systematic importance, remarking that "the typical *communis* also has numerous teeth on the labrum." However, I most emphatically dissent from his opinion in this respect. As he says, it is true that the balanids are highly variable as far as a particular character is concerned, but I hold that there are certainly some admittable limitations in the range of variation. A similar unreliability in identifications based only on the labrum was pointed out by Pilsbry (1916: 88), in the case of *Balanus improvisus*.

Some specimens of subspecies *communis* resemble subspecies *hawaiiensis* superficially, being often found together in the same place, but

TABLE 1

THE NUMBER OF LONGITUDINAL COLORED STRIPES IN ALL COMPARTMENTS OF *Balanus amphitrite hawaiiensis* AND *Balanus amphitrite communis**

SIZE OF SPECIMENS	CARINA	LEFT CARINO-LATERAL COM-PART-MENT	RIGHT CARINO-LATERAL COM-PART-MENT	LEFT LATERAL COMPART-MENT	RIGHT LATERAL COMPART-MENT	ROSTRUM
B. a. hawaiiensis						
c.r.d. 15.4 mm.	(0)5(1)5(1)	(1)2(1)	(0)2(2)	(1)4(2)4(1)	(0)5(1)4(2)	(2)5(2)5(2)
c.r.d. 18.0 mm.	(1)3(2)4(1)	(1)2(1)	(1)2(2)	(2)4(2)4(1)	(1)5(2)4(2)	(2)5(3)6(1)
c.r.d. 18.5 mm.	(0)5(2)4(0)	(0)3(1)	(1)2(1)	(2)5(1)3(1)	(1)4(1)4(0)	(2)4(2)4(3)
c.r.d. 19.6 mm.	(2)4(1)3(1)	(1)2(1)	(1)2(1)	(1)3(3)4(2)	(2)2(2)2(0)	(1)5(2)4(2)
B. a. communis						
c.r.d. 14.0 mm.	10	3	2	10	9	9
c.r.d. 18.2 mm.	8	2	2	9	9	9
c.r.d. 20.0 mm.	9	4	2	10	10	10

* c.r.d. = carino-rostral diameter. Numbers without parentheses represent distinct stripes. Numbers in parentheses represent obsolete or reduced stripes. The total number corresponds with the number of parietal tubes in each of the compartments.

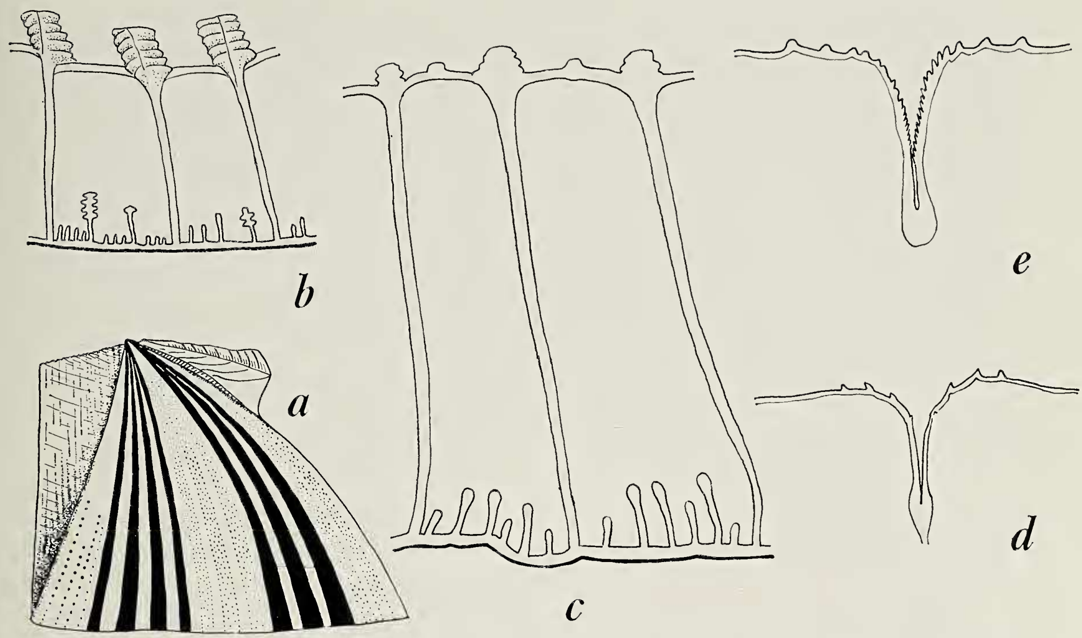

FIG. 1. *Balanus amphitrite hawaiiensis* Broch (*a, b* and *e*) and *B. amphitrite communis* Darwin (*d*): *a,* Profile of left lateral compartment, showing the arrangement of longitudinal colored stripes, either distinct or indistinct (dotted in the figure); *b, c,* basal view of parietal tubes; *d, e,* labrum.

the two differ in several important details of structure, as summarized in Table 2.

Consideration of these characteristics will prove that the two subspecies are separable from each other when large series of specimens are examined.

DISTRIBUTION AND SYNONYMY

Herewith is presented a summary of accounts of the corresponding subspecies of *Balanus amphitrite* Darwin given by previous workers and the supposed geographical distribution of *B. amphitrite hawaiiensis* Broch (Fig. 3). The evidence is far from complete and some records of occurrence are not conclusive, since most of the subspecies or forms of *Balanus amphitrite,* especially the most familiar *communis,* have been insufficiently described (often without detailed figures), or are recorded only by a subspecific name. Nevertheless, those I have listed may help future workers towards the solution of the problems presented herein.

1. Recorded as *B. a. hawaiiensis:*

   Kaladis Point, Mindanao (Broch, 1922).
   Pearl Harbor, Hawaii (Broch, 1922).
   Honolulu Harbor, Hawaii (Pilsbry, 1928).
   Sasebo, Kure, Maizuru, Seto, and Misaki, Japan (Hiro, 1937, 1938).
   Persian Gulf (Nilsson-Cantell, 1938).
   Suo, Kiirun, Tansui, Takao, and Mako, Formosa (Hiro, 1939).
   Aio, Seto Inland Sea, Japan (Hudinaga and Kasahara, 1942).
   Pearl Harbor and Kaneohe Bay, Hawaii (Edmondson and Ingram, 1939; Edmondson, 1946).
   Misaki, Japan (Hirano and Okushi, 1952).

2. Recorded as *B. a. denticulata:*

   Suez Canal (Broch, 1927; Ciurea *et al.,* 1933; Monod, 1937).
   Southern coasts of Britain (Bishop, 1950; Norris *et al.,* 1951; Crisp and Molesworth, 1951).
   Atlantic coasts of France (Bishop *et al.,* 1957).
   Knysha Estuary, South Africa (Millard, 1950).

Queensland and Torres Strait, Australia (Allen, 1953).
Durban Bay, South Africa (Day and Morgan, 1956).

3. Recorded as *B. a. communis* (in part):
Ismailia, Timsah Sea, Suez Canal (Nilsson-Cantell, 1921).
? Billiton, Sunda Islands (Nilsson-Cantell, 1921).
? Messina port, Italy (Nilsson-Cantell, 1921).
Istanbul harbor, Turkey (Neu, 1939).
Middle Harbor, Port Jackson, Australia (Pope, 1945).
Adriatic Sea (Kolosváry, 1947).
Black Sea (Zevina and Tarasov, 1957).

4. Recorded as *B. a. venustus:*
Krusadai, Gulf of Manaar, Ceylon (Raj, 1927).

5. Recorded as *B. a. franciscanus* and *B. a. herzi:*
San Francisco Bay, California (Rogers, 1949).[3]

6. Recorded as *B. amphitrite,* subspecific name not given:
Atlantic coasts of France (Prenant, 1929; Fischer, 1929; Fischer-Piette, 1932, etc.).
? Biscayne Bay, Florida (Weiss, 1948).
Oakland Estuary, California (Graham and Gay, 1945).

7. Unpublished records of occurrence:
San Diego, Salton Sea, and San Francisco Bay, California; and the Hawaiian Islands (Newman, 1955, 1956: personal communication).
Dakar, West Africa (from I.F.A.N. Collection).
Seto Inland Sea and Ise Bay, Japan (Ota, 1955: personal communication).

A detailed discussion of the synonymies listed above is omitted, for the sake of saving space, but the preceding illustrations and descriptions

[3] I am not certain whether another new subspecies, *B. a. saltonensis* Rogers, from the Salton Sea, is the same as the others or is distinct from them.

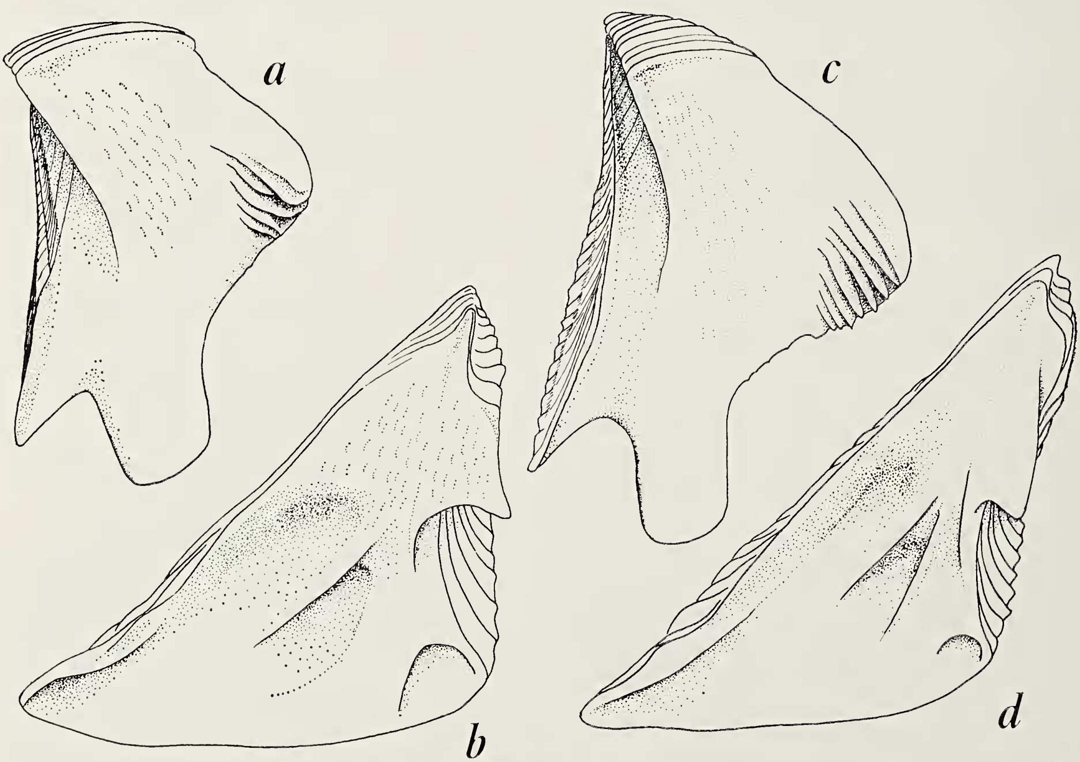

FIG. 2. *Balanus amphitrite hawaiiensis* Broch (*a* and *b*) and *B. amphitrite communis* Darwin (*c* and *d*): *a* and *c*, Inside of tergum; *b* and *d*, inside of scutum.

TABLE 2

DIFFERENCES IN DETAILS OF STRUCTURE BETWEEN *Balanus amphitrite hawaiiensis* AND *B. amphitrite communis*

DETAILS OF STRUCTURE	*B. amphitrite hawaiiensis*	*B. amphitrite communis*
Ground color of shell...	Glossy white	Rather reddish white, darkened with bluish tint in upper part
Outside of parietes........	Only dark violet longitudinal stripes sharply defined; those in middle and along both sides indistinct or reduced (Fig. 1*a*)	Pale or dark violet longitudinal stripes crossed by the same colored or reddish transverse stripes on the whole area
Inside of parietes..........	Strongly ribbed up to the sheath; ribs flat on roof and finely denticulate on both sides but not bifurcate distally (Fig. 1*b*)	Slightly ribbed near base; ribs low, with slight denticulation at base which may extend as bifurcate secondary ribs; a few shorter riblets often interseptally (Fig. 1*c*)
Parietal tubes................	Numerous (about 16 in rostrum), narrow and square at base (Fig. 1*b*)	Few (about 9 in rostrum), large and rectangular at base (Fig. 1*c*)
Radii............................	Very broad, flat, with almost level summits, forming an angle of about 100°–110° with the interlocking margin (Fig. 1*a*)	Narrow, slightly sunken, with very oblique summits, forming an angle of about 140° with the interlocking margin
Rostrum.........................	Apex usually incurved	Apex often turned outwards when isolated
Scutum..........................	Depression below adductor ridge deep, oblongly circumscribed (Fig. 2*b*)	Depression below adductor ridge shallow, lengthened along adductor ridge (Fig. 2*d*)
Tergum..........................	Spur very broad, over ⅓ width of the valve, short, either rounded or truncate distally and separated from basi-scutal angle by less than its own width; crests for depressor muscles strongly developed, typically 5 (Fig. 2*a*)	Spur longer than wide, with more or less hatchet-shaped end, separated from basi-scutal angle by its own width which is less than ⅓ that of the valve; crests for depressor muscles not so strong, exceeding 5 in number (Fig. 2*c*)
Labrum..........................	Multidenticulate on each side of a median notch (Fig. 1*e*)	3 teeth, or with a smaller additional one, on each side (Fig. 1*d*)

of this subspecies, compared with the typical *communis,* will help to a certain extent in later identifications.

NATIVE SEA AND HABITAT

From these data of occurrence, it is very likely that the subspecies *hawaiiensis* (= *denticulata*) is not a local variant restricted to such a small area of special environments as the Suez Canal, but nowadays is very widely distributed in circumequatorial tropical and temperate areas in all oceans.

Its native habitat is probably the Hawaiian Islands in the mid-Pacific tropical sea. From this mid-Pacific area it may have spread much earlier and more rapidly in all seas than did the Australasian barnacle, *Elminius modestus* Darwin, in European and South African waters. It is supposed that the first establishment of this Hawaiian barnacle took place from the tropical west Pacific, such as the Philippines and Formosa, lying along the North Equatorial Current, where it is directed westerly, although the most probable means of migration may have been attachment on the hulls of ships.

In these tropical and subtropical areas the

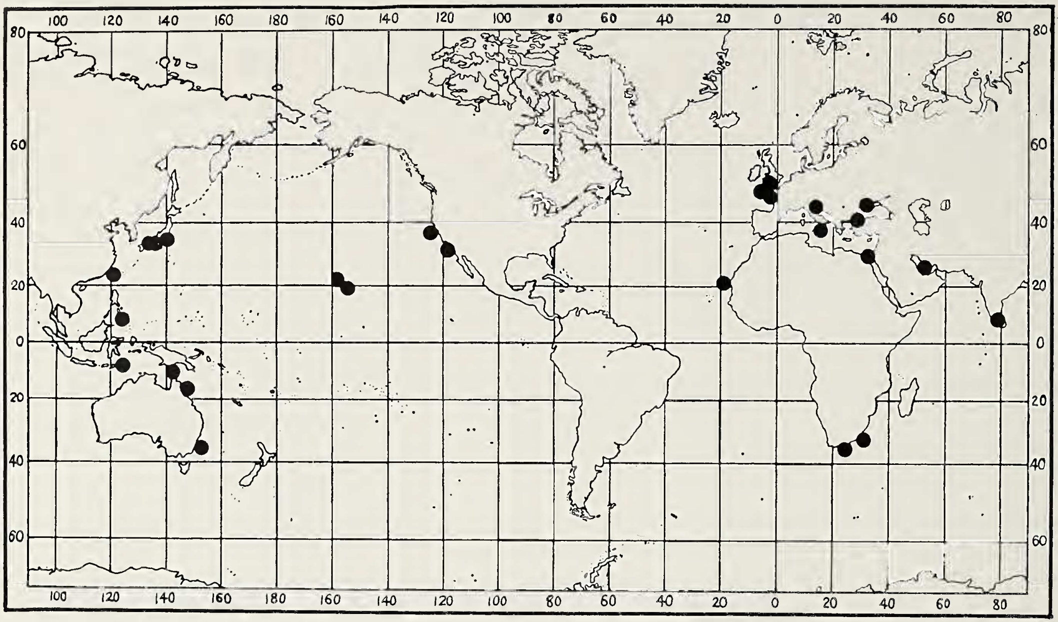

FIG. 3. Geographical distribution of *Balanus amphitrite hawaiiensis* Broch.

barnacles grow abundantly in the intertidal zone of sheltered coasts, usually below the mean sea level; sometimes they occur in clusters on wharf piles, coastal rocks, and mangrove roots on the leeward side but not on seaward reefs with flourishing reef corals.

In the more northern temperate areas, such as the Japanese and Californian coasts, the barnacles are generally restricted to quiet bays or harbors of enclosed water and are usually attached to floats, buoys, ship bottoms, or submerged panels under the low tide level.

They seem to have a tolerance for a wide range of salinities (on the average S 16–30 °/oo), for they are found in the main harbor waters where the salinity is that of normal sea water but may be subject to at least occasional dilution with fresh water. In more estuarine situations they are replaced by *B. amphitrite albicostatus* Pilsbry or by *B. amphitrite krügeri* Nilsson-Cantell. On the other hand, in more saline waters towards the mouth of bays, *B. amphitrite communis* as well as *B. trigonus* Darwin dominate in the subtidal zone. A similar change in barnacle communities has been noted by Day and his collaborators (1956) during their ecological survey of South African estuaries.

From my experience of studies on the fouling organisms of naval ships, I am reminded that *B. amphitrite hawaiiensis* was predominant in Kure port, on the Seto Inland Sea, but was less common in any of the bays facing open seas along the Pacific coast of Japan. There the dominant form was *B. amphitrite communis.*

In this connection it is interesting to find a similar change of habitats in *B. amphitrite denticulata* (= *B. a. hawaiiensis*) established on the Atlantic coasts of France (Bishop *et al.,* 1957). According to them, it is always submerged on the northern coast but is rare or absent on the southwestern coasts of highly estuarine condition.

From these ecological evidences, it seems most appropriate to say that *B. amphitrite hawaiiensis* is a protected-water form rather than a polyhaline form. *B. amphitrite communis,* on the other hand, is a stenohaline subtidal form; and *Elminius modestus* is a more estuarine intertidal form. This last-named barnacle was originally found in a temperate habitat, in European waters, where it had established itself, so that it may extend farther northward than does *B. amphitrite hawaiiensis.*

At any rate, marine animals living in an environment of variable salinity have their reproductive cycle of spawning correlated with the temperature cycle rather than with salinity. Therefore, as might be expected, there is no particular correlation between successful establishment of fouling organisms and the variable salinity of sea water in the different regions where the barnacle makes a successful settlement.

SUPPLEMENTAL NOTE

After the present paper was submitted, an article by John D. Costlow and C. G. Bookhout, entitled "Larval development of *Balanus amphitrite* var. *denticulata* Broch reared in the laboratory," appeared in the Biological Bulletin, 114(3): 284–295, June, 1958. In this paper they confirmed the fact that *B. amph. denticulata* occurs abundantly as an important fouling organism at Beaufort, North Carolina, on the east coast of North America, and that it is wholly identical with *B. amph. hawaiiensis* in all naupliar stages during metamorphosis. The occurrence of this subspecies there may be supposed also from the illustrations given in Weiss (1948).

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